

Food habits and trophic niche overlap of the Badger (*Meles meles* L.) and the Red fox (*Vulpes vulpes* L.) in a Mediterranean coastal area¹

By BARBARA CIAMPALINI and S. LOVARI

Dipartimento di Biologia Ambientale dell'Università di Siena and Istituto di Zoologia dell'Università di Parma, Italia

Receipt of Ms. 5. 11. 1984

Abstract

Studied the diets of badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) in a coastal area of West-central Italy, using faecal analysis, throughout a year. Both volume and frequency of occurrence of different foods were quantified. Arthropods were the staple of both species in spring and summer, whereas fruits were the most important resource in autumn and winter. The diet overlap of badgers and foxes proved very extensive, in spite of minor differentiating details.

Introduction

While there is a wealth of information on the food habits of badgers and foxes in North and Central Europe (Badgers: e.g. ANDERSEN 1955; SKOOG 1970; KRUK and PARISH 1981; Foxes: e.g. ENGLUND 1965; GOSZCZYNSKY 1974; MATEJKA et al. 1977), little is known of their diets in the Mediterranean area. The only available data on badgers come from studies carried out in mountain ranges (IBAÑEZ and IBAÑEZ 1980; KRUK and DE KOCK 1981), where environmental conditions tend to be comparable with those at higher latitudes. Nothing at all has been published on lowland badgers. Yet it is where the warmer climate occurs and there is a richer variety of potential food resources, i.e. in Mediterranean lowlands, that the greatest diet differences may be expected because of the basically distinct environmental features. One could also expect that, in an area with many different, potential foods available throughout the year, the feeding habits of a "specialist" species may be more likely to shift towards the exploitation of different resources seasonally available, and vice versa. In fact, while the Red fox has been usually reported as a "generalist" species (cf. the above mentioned authors), i.e. with broad food preferences, the badger has recently been defined as basically an earthworm specialist which occasionally makes use of opportunities provided by the availability of other foods (KRUK and PARISH 1981). Furthermore, BROWN (1983) suggested that the abundance of earthworms may limit the badger numbers in some areas of North-east Scotland. On the other hand, MOUCHÉS (1981) reported from West France that badgers feed upon a wide range of food items, yet he also confirmed their definite seasonal preference for earthworms.

As to the fox, there are only a few published studies on its food habits in Southern Europe, and again nearly all are concerned with mountain areas: the Western Sierra Morena (AMORES 1975) and the Western Cordillera Cantabrica (BRAÑA and DEL CAMPO

¹ Research supported by the Maremma Natural Park Administration and by a contribution from the Italian Ministry of Education.

1980) in Spain, as well as the Western Alps (LEINATI et al. 1960) in Italy. Just one report, relevant to the months of January, February and March only, is available for the Mediterranean lowlands (POZIO and GRADONI 1981).

Finally, no study has been produced so far to assess and to measure the overlap of exploitation of food resources in foxes and badgers in the same area. Yet, the trophic niche differentiation of these similar-sized carnivores may be an important factor to allow the survival of both species where they live in sympatry.

The aims of our study were to determine qualitatively and quantitatively the food habits of the badger and the fox in a lowland, Mediterranean area, to evaluate the extent of the trophic niche overlap of these species, and to assess whether the feeding specialisation of the badger as an earthworm predator is still maintained in an area where presumably many different food resources are seasonally available.

Material and methods

Between April 1982 and April 1983 a total of 188 scats of badgers (sample size: D-J, N=47, F-M, N=30; A-M, N=19; J-J, N=18; A-S, N=36; O-N, N=38) was collected in successive visits, every fortnight, from the characteristic "latrines" distributed along a fixed 6-km itinerary throughout our study area. While searching for badger faeces, we also collected 208 fox scats (sample size: D-J, N=40; F-M, N=42; A-M, N=17; J-J, N=28, A-S, N=40; O-N, N=41). The excrements were stored in polythene bags and deep-frozen, to be thawed later on and analysed as described in KRUK and PARISH (1981). Each sample was washed in a tea-sieve, 1.3 mm mesh, and the sediment in the rinsing water was searched under a binocular microscope to detect the occurrence of earthworm chaetae. Then, the washed sample was inspected in a large dish and the total numbers of each kind of food were counted and/or estimated. The relative volume of each kind of food, estimated by eye, was scored for each sample on a seven point scale and the mean values of these seven categories were used in the final evaluation of the ingested volume. Relevant details are given in KRUK and PARISH (1981).

Data were worked out as 1. frequency of occurrence; 2. estimated volume of each food category whenever it was eaten (cf. KRUK and PARISH 1981; KRUK and DE KOCK 1981).

Correlations between temperature (Fig. 1) and occurrence of each food item in the diet were tested using the Spearman rank correlation coefficient (SIEGEL 1956).

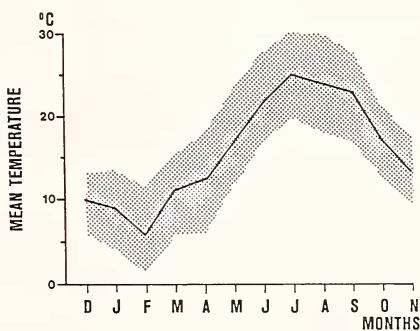


Fig. 1. Mean monthly variation and range (shaded area) of temperature (°C) in the study area throughout the research period

Study area

Our study area lay at sea-level in the Maremma Natural Park, Grosseto county, along the Tyrrhenean coastline, Central Italy (42°39' N/11°05' E). Our itinerary passed through, or near, all the main vegetation types of the Mediterranean coast: meadows, maquis, pine woods and wetland. No shooting and no use of pesticides were allowed in the park, so that animals could feed whenever they wished and the Arthropods were naturally abundant. For a description of the vegetation and geo-morphology of the area, see ARRIGONI et al. (1976).

Results

Badger

Fig. 2 shows the frequency of occurrence (%) of seventeen main food categories throughout the year. Large Lamellicornia beetles (*Scarabaeidae: Geotrupes* spp., *Melolonthinae*, *Cetoniinae*, etc.) were very important items of the diet at all times of year: as larvae, especially from February (included) to June; as adults, mainly from June (included) to December. Other arthropods proved also to be important temporary food resources:

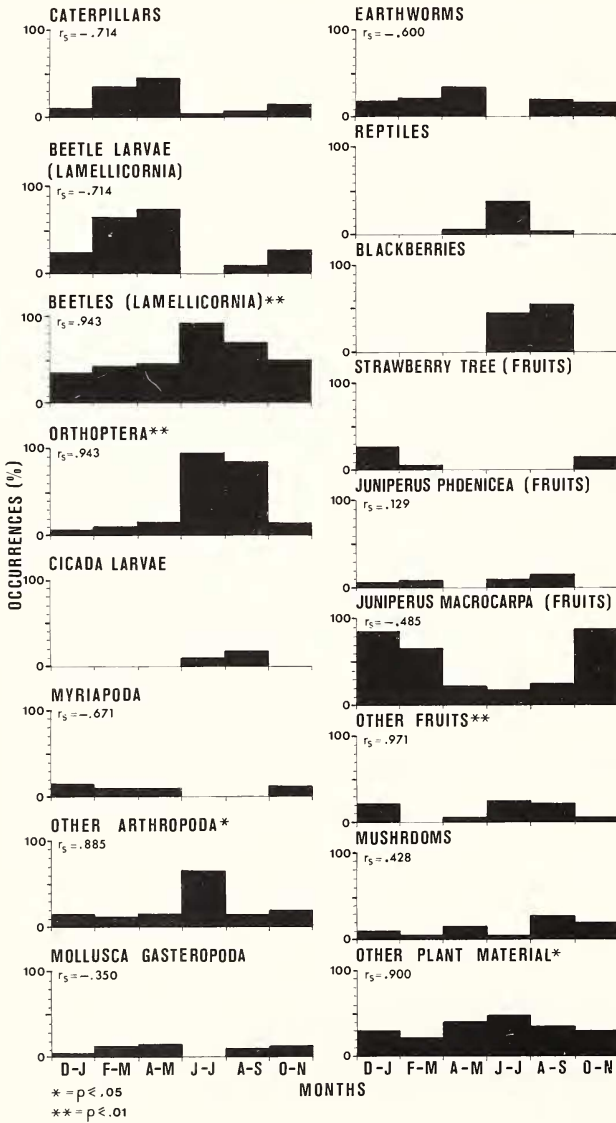


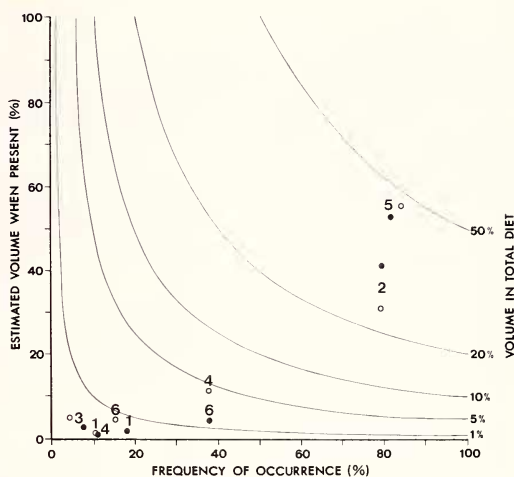
Fig. 2. Percentage of occurrences of food categories in the badger diet over a year. Correlation values refer to mean temperature

grasshoppers appeared at a high percentage from June to October, whereas caterpillars were abundant in the diet in late winter and spring. On the whole, the occurrence of earthworm chaetae was fairly rare and these worms could hardly be considered a major food resource in our study area. The occurrence of adult Lamellicornia, Orthoptera and other Arthropoda in scats was directly correlated with temperature.

While blackberries (*Rubus* sp.), fruits of the strawberry tree (*Arbutus unedo*) and others were usually taken in short periods of the year, when ripe, the berries of *Juniperus macrocarpa* were the staple food during all the autumn and winter months, and they were also taken – although more rarely – in spring and summer.

Fig. 3 shows the frequency of occurrence and relative volume of food categories in samples pooled over the whole year. We found it somewhat hard to estimate objectively, by eye, the relative volume of some foods (e.g. vertebrates, other plant material). So, we feel that such data should be interpreted with caution,

Fig. 3. Estimated volume of badger (solid circles) and fox (open circles) food categories, whenever eaten, versus their frequency of occurrence. Isopleths connect points of equal relative volume in the overall diet. Annual data. 1 = Earthworms; 2 = Arthropods; 3 = Other Invertebrates; 4 = Vertebrates; 5 = Fruits; 6 = Other Plant Material



especially with regard to the less common kinds of food. Some minor components of the diet, from grass to plastics, were not plotted in the diagram as, although sometimes they provided bulk, they were likely to have been swallowed while feeding on other food items. In spite of such limitations, these data provide an approximate, but still useful idea of the importance of the major diet components.

Over the whole year, fruits and arthropods were the most important food categories, both lying between the 25% and 45% isopleths in Fig. 3. In spring (Table 1) arthropods were by far the major food resource while in summer fruits began to grow in importance until they took the lead in autumn and winter.

Fox

Fig. 4 shows that the berries of *Juniperus macrocarpa* were the staple diet of the fox throughout the whole year with a relative fall in the summer months. The use of such berries proved to be inversely associated with temperature. The same correlation was also found for pine seeds. Mammals (mostly rodents, 38–40%), caterpillars (12.2–40%) and earthworms (20–26%) were eaten mainly in winter and spring, whereas the numbers of grasshoppers built up greatly in the summer months and their occurrence in scats was directly correlated with temperature. Other important summer foods were medium and large-sized beetles (chiefly Scarabaeidae) and, in late summer, also blackberries (5.9% in July; 40.9% in August; 22.2% in September) and berries of *Juniperus phoenicea* (35%). Beetle larvae kept always at fairly high levels (about 30%) except in June–July.

Plotting the estimated volume of the major categories versus their frequency of occurrence (%), fruits and to a lesser extent arthropods proved to be the main food resources of the fox over the whole year (Fig. 3). Arthropods were the staple food in spring, followed by fruits, other plant material and vertebrates (Table 1); their importance grew further in summer when vertebrates and particularly other plant material fell down. A remarkable shift was observed in the autumn: consumption of fruits built up greatly whereas the other categories decreased accordingly. In winter, the importance of vertebrates in the fox diet increased again, although fruits (*Juniperus macrocarpa*) still remained the staple item.

Trophic niche breadth and overlap

To evaluate the trophic niche breadths of the badger and the fox as well as their overlap in our study area, we used respectively the LEVINS (1968) and PIANKA (1973) indices, as

Table 1

Percentages of the estimated volume of each food category, whenever it was eaten, and percentages of frequency of occurrence in all faeces, for the badger and the red fox
Seasonal data. Food categories as in Fig. 3 (7 = Other)

Estimated volume (%)	Spring	Summer	Autumn	Winter
Badger				
1	0.74	0.62	0.45	0.98
2	64.96	59.49	23.94	33.88
3	1.01	0.30	0.27	0.49
4	0.89	1.57	0.42	0.10
5	18.42	36.61	73.05	62.45
6	13.97	0.97	1.79	2.09
7	—	0.41	—	—
Red fox				
1	0.35	—	0.26	0.78
2	44.65	53.09	9.62	19.93
3	1.19	—	0.09	0.12
4	20.80	8.04	4.05	14.81
5	17.43	38.75	84.53	59.96
6	15.00	0.09	1.26	4.10
7	0.55	—	0.17	0.26
Frequency of occurrence (%)				
Badger				
1	33.33	13.46	16.94	16.07
2	85.71	90.38	64.40	80.35
3	14.28	7.67	10.16	8.92
4	9.52	19.23	6.77	3.57
5	38.09	80.76	96.91	82.14
6	42.85	44.23	42.37	28.57
7	—	7.69	—	—
Red fox				
1	14.28	—	9.83	20.63
2	75.00	100	72.13	66.66
3	14.28	—	3.27	4.76
4	39.28	47.36	19.67	50.79
5	64.28	68.42	98.36	93.65
6	50.00	3.50	6.55	14.28
7	3.57	—	4.91	1.58

suggested by RICKLEFS (1980) and PUTMAN and WRATTEN (1984), on the frequency of occurrences of the food categories² (Table 2). We set the total number of occurrences as 100 % to fulfill the assumption of such indices.

The niche breadth of the fox was at its maximum in spring and at its minimum in the

² Levins Index:

$$B = \frac{1}{\sum_{i=1}^n p_i^2}$$

where p_i is the proportion of records for a species in each category (i) of the food niche. *Low niche breadth*: 1; *great niche breadth*: n (number of food categories).

Pianka Index:

$$O_{jk} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}}$$

where p_{ij} is the proportion of species j's activity recorded from category i of the food dimension.

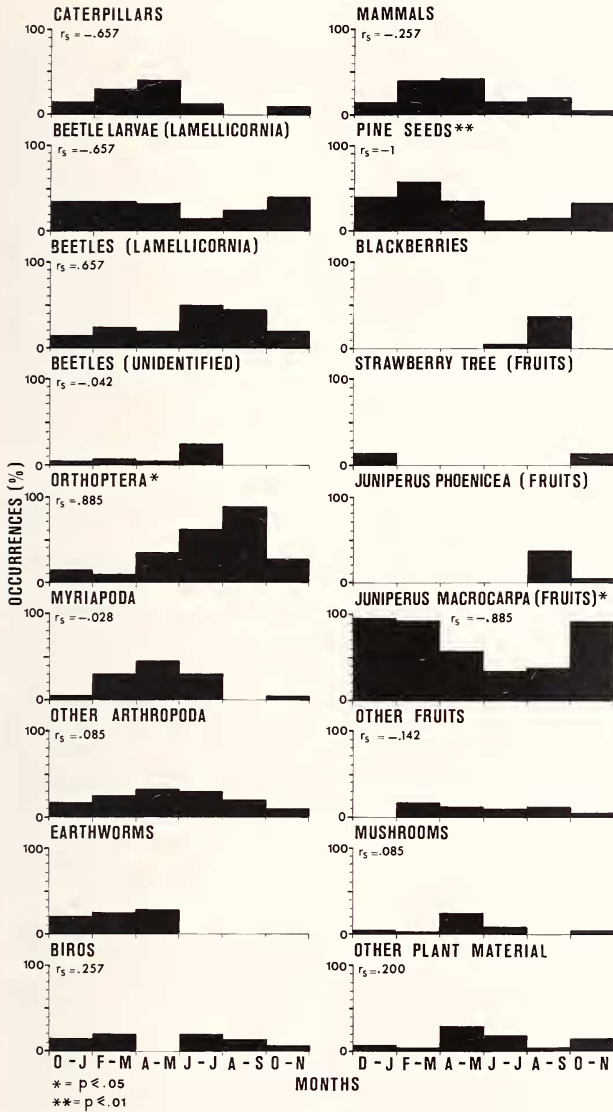


Fig. 4. Percentage of occurrences of food categories in the fox diet over a year. Correlation values refer to mean temperature

that the amount of insects eaten in autumn and winter by several species of birds of prey and owls, in Central Italy, proved far greater than in Central and Northern Europe, where vertebrates were the staple food. One could also predict that items rich in oils and sugar, such as *macrocarpa* berries and pine seeds, will be favoured as foods in the cold season, when caloric requirements are greatest. Furthermore, one may expect that the digestive system of a carnivore will not be able to exploit fully the nutrients contained in plant materials. This, in turn, could lead to an increased ingestion of such food to compensate for its relative indigestibility, especially when 1. that food contains important nutrients, and 2. there may be a decrease of alternative food resources i.e. in the cold months. Finally,

autumn, whereas the badger did not show any seasonal variation. On the other hand, the degree of overlap between the two species proved very high both annually (0.83) and seasonally, never being far from the top value of overlap (1.0): in spring there was minimum overlap (0.77) and in autumn there was maximum overlap (0.91) (Table 2). The annual index of overlap was even higher when volumetric measures were used: 0.98.

Discussion

Our data confirm the opportunistic foraging habits reported by many authors for red foxes (e.g. ENGLUND 1965; HALTENORTH and ROTH 1966; AMORES 1975) which will eat whatever food is available locally. One could expect that a 'generalist' will start eating large numbers of arthropods in an area where these are abundant, as in the lowland Mediterranean country where environmental factors, e.g. mild winters and rich plant communities, favour the availability of insects (BLONDEL 1969). In fact, LOVARI (1974) has shown

Table 2

Seasonal and annual trophic niche breadths (Levins 1968) and overlap (Pianka 1973) of the badger and the red fox, based on percentage of occurrences
Top value of overlap = 1

	Badger		Red fox		Trophic niche Overlap 0
	B	F.C. (No.)	B	F.C. (No.)	
Spring	9.31	15	13.29	17	0.77
Summer	10.72	19	9.19	16	0.88
Autumn	8.21	18	7.33	20	0.91
Winter	10.17	17	9.70	19	0.86
Annual	9.35	22	11.29	21	0.83

B = Levins Index, 0 = Pianka Index, F.C. = Food Categories

resources rich in proteins (mammals, birds) may be expected in the diet of a carnivore especially during pregnancy, when females have to grow foetuses, and in the first weeks after parturition, when milk and transportable, substantial food items must be provided for the cubs. Our results are consistent with such expectations.

On the other hand, the diet of badgers proved strikingly different from that reported by previous authors. Earthworms occurred in badger scats nearly all year long except in the hottest summer months, when presumably these worms were less available (or less sought after) because of the drought (or because other items became abundant: arthropods, some fruits). Yet their bulk in the diet proved almost nil, which strongly differs from the findings of other authors (e.g. Sweden: SKOOG 1970; Denmark: ANDERSEN 1955; Netherlands: WIERTZ, 1976, in KRUIK and PARISH 1981; Great Britain: e.g. NEAL 1977; KRUIK and PARISH 1981; France: MOUCHÉS 1981; Spain: IBÁÑEZ and IBÁÑEZ 1980; Italy: KRUIK and DE KOCK 1981).

However, it may be worth pointing out that worms tend to be restricted in importance as a key-food to definite seasons especially in central and southern areas of Europe, while at other times of year other resources replace them in the diet: cereals and fruits in West France (MOUCHÉS 1981), amphibians and fruits in North Spain (Sierra de Cameros: IBÁÑEZ and IBÁÑEZ 1980), olives in North Italy (Mt. Baldo: KRUIK and DE KOCK 1981). Our study has shown that badgers depend on two major food categories all year long: arthropods are the staple in spring and summer, while fruits follow rather closely; fruits become the major food resource in autumn and winter, while arthropods are still widely eaten. Furthermore, if such broad categories are broken down into smaller ones (taxa lower than arthropods; fruit species), the trophic niche of the badger proves to be as extensive as that of the fox, which does not support the view of a specialist predator of earthworms (KRUIK and PARISH 1981, 1982). Our results are also supported by data collected from April 1983 onwards, in the same area (PIGOZZI, in prep.). Therefore, such findings are unlikely to be biased.

KRUIK and PARISH's model (1982, predicting that, where patches of earthworms are scattered, the territories of badgers are bigger and that, where patches are richer in earthworms, the 'clans' of badgers are larger) could be interpreted as the adaptation of a generalist species to a rewarding and geographically abundant food resource, the earthworm, rather than being a species-specific feature. In fact, group size and social organisation of the badger in Maremma would seem to differ considerably (PIGOZZI, in preparation) from what known so far for Northern badgers (NEAL 1977; KRUIK 1978), being closer to the 'asocial' organisation of most mustelids.

Competition between two species occurs when individuals use a common, scarce resource and when increase in the number of either decreases the fitness of the other. It is beyond doubt that foxes and badgers utilise nearly all the same trophic resources in Maremma. Unfortunately our data do not allow any conclusion on actual food competition between such species and further, long-term research will be needed to find it out.

Acknowledgements

We are most grateful to H. KRUK for his encouragement to undertake this study and for his comments on the second draft of our paper. T. CARO, I. J. PATTERSON and T. ROPER kindly took the time to comment on the first draft and to revise our English. M. CALISTI helped greatly in the scat analysis, whereas G. PIGOZZI provided constructive discussions on the evaluation of our results. We are indebted to GABRIELLE OETTINGEN for her help in the translation of the German summary. Finally, I. BOSCHI, director of the Maremma Natural Park, made this study possible with his helpful collaboration at all stages of our research. This paper was written during a one-year leave of the second author at the Sub-Department of Animal Behaviour, Cambridge University.

Zusammenfassung

Nahrung und Nahrungsüberschneidung bei Dachs (Meles meles L.) und Fuchs (Vulpes vulpes L.) in einem mediterranen Küstengebiet

In einem Küstengebiet im westlichen Mittelitalien wurden von April 1982 bis April 1983 Kotproben von Dachs und Fuchs gesammelt und analysiert. Volumen und Häufigkeit des Auftretens der verschiedenen Nahrungsbestandteile wurden ermittelt. Anders als in Nord- und Mitteleuropa frisst der Dachs in Italien eine Vielzahl verschiedener Nahrungsarten und nicht in erster Linie Regenwürmer. Früchte bildeten im Winter, Arthropoden im Frühjahr und Sommer seine Hauptnahrung. Die Nahrung des Fuchses war ähnlich, doch fraß er (im Winter mehr, im Frühjahr weniger) mehr Vertebraten als der Dachs. Aber auch bei ihm überstieg der Wirbeltieranteil nie 10 Volumenprozent. Die häufigste Pflanzennahrung beider Arten waren Beeren von *Juniperus macrocarpa*. Blatthornkäfer (Lamellicornia), vor allem Scarabaeidae wurden während des ganzen Jahres aufgenommen. Ihre Larven wie auch Schmetterlingsraupen erreichten beim Dachs ein Maximum im Frühjahr und blieben beim Fuchs ständig häufig. Sie gingen nur im Juni und Juli zurück, als Käfer-Imagines ein Maximum erreichten. Dachs und Fuchs überschneiden sich stark in der Futterwahl (0,83) und ernährten sich von einer Vielzahl verschiedener Nahrungsarten. Danach sind beide Arten bezüglich ihrer Ernährung Generalisten.

References

- AMORES, F. (1975): Diet of the Red Fox (*Vulpes vulpes*) in the Western Sierra Morena (South Spain). Doñana Acta Vertebrata 2, 221-239.
- ANDERSEN, J. (1975): The Food of the Danish Badger (*Meles meles danica*) with Special Reference to the Summer Months. Dan. Rev. Game Biol. 3, 1-75.
- ARRIGONI, P. V.; GELLINI, R.; INNAMORATI, M.; LENZI-GRILLINI, C.; LOVARI, S.; PIUSI, P.; RENZONI, A.; SANESI, G.; SARTONI, G. (1976): Relazione al Consorzio per l'istituzione del Parco della Maremma. Inf. Bot. Ital. 8, 283-324.
- BLONDEL, J. (1969): Sédentarité et migration des oiseaux dans une garrigue méditerranéenne. Terre et Vie 23, 269-314.
- BRAÑA, F.; DEL CAMPO, J. C. (1980): Estudio de la dieta del Zorro (*Vulpes vulpes*, L.) en la mitad occidental de la Cordillera Cantabrica. Bol. Ciencias Naturales I. D. E. A. 26, 135-146.
- BROWN, C. A. J. (1983): Prey Abundance of the European Badger (*Meles meles* L.) in North-east Scotland. Mammalia 47, 81-86.
- ENGLUND, J. (1965): Studies on Food Ecology of the Red Fox (*Vulpes vulpes*) in Sweden. Viltrevy 3, 375-485.
- GOSZCZYNSKY, J. (1974): Studies on the Food of Foxes. Acta Theriol. 19, 1-18.
- HALTENORTH, T.; ROTH, M. H. (1968): Short Review of the Biology and Ecology of the Red Fox. Säugetierk. Mitt. 16, 339-352.
- KRUK, H. (1978): Spatial Organisation and Territorial Behaviour of the European Badger *Meles meles* L. J. Zool., Lond. 184, 1-19.
- KRUK, H.; DE KOCK, L. (1981): Food and Habitat of Badgers (*Meles meles* L.) on Monte Baldo, Northern Italy. Z. Säugetierkunde 46, 295-301.
- KRUK, H.; PARISH, T. (1981): Feeding Specialisation of the European Badger (*Meles meles* L.) in Scotland. J. Anim. Ecol. 50, 773-788.

- KRUUK, H.; PARISH, T. (1982): Factors Affecting Population Density, Group Size and Territory Size of the European Badger, *Meles meles*. J. Zool., Lond. 196, 31–39.
- IBÁÑEZ, C.; IBÁÑEZ, J. I. (1980): Alimentación del tejón (*Meles meles* L. 1758) en el Rasillo de Cameros (Logroño, España). In: 1ª Reunion Ibero-amer. Zool. Verteb., La Rábida 1977, Spain, 517–527.
- LEINATI, L.; MANDELLI, G.; VIDESOTT, R.; GRIMALDI, E. (1960): Indagini sulle abitudini alimentari della volpe (*Vulpes vulpes* L.) nel Parco Nazionale del Gran Paradiso. Clinica Veterinaria 83, 1–24.
- LEVINS, R. (1968): Evolution in Changing Environments. Princeton N. J.: Princeton Univ. Press.
- LOVARI, S. (1974): The Feeding Habits of Four Raptors in Central Italy. Raptor Research 8, 45–57.
- MATEJKA, H.; RÖBEN, P.; SCHRÖDER, E. (1977): Zur Ernährung des Rotfuchses *Vulpes vulpes* (Linné, 1758) im offenen Kulturland. Z. Säugetierkunde 42, 347–357.
- MOUCHÉS, A. (1981): Variations saisonnières du regime alimentaire chez le blaireau européen (*Meles meles* L.). Rev. Ecol. (Terre et Vie) 35, 183–194.
- NEAL, E. G. (1977): Badgers. London: Blandford.
- PIANKA, E. R. (1973): The Structure of Lizard Communities. Ann. Rev. Ecol. Syst. 4, 53–74.
- POZIO, E.; GRADONI, L. (1981): Spettro trofico della volpe (*Vulpes vulpes* L.) e della faina (*Martes foina* Erxl.) in provincia di Grosseto. Natura 72, 185–196.
- PUTMAN, R. J.; WRATTEN, S. D. (1984): Principles of Ecology. London: Croom-Helm.
- RICKLEFS, R. E. (1980): Ecology. Middlesex: Nelson & Sons.
- SKOOG, P. (1970): The Food of the Swedish Badger (*Meles meles* L.). Viltrevy 7, 1–120.
- IEGEL, S. (1956): Nonparametric Statistics. New York: McGraw-Hill.

Authors' addresses: Dr. SANDRO LOVARI, Istituto di Zoologia, Strada dell'Università 12, I-43100 Parma, and BARBARA CIAMPALINI, Via G. Pietri 5, I-53100 Siena

Cephalisation bei Feliden

Von M. RÖHRS^{1,2}

Institut für Zoologie der Tierärztlichen Hochschule Hannover

Eingang des Ms. 8.3.1985

Abstract

Cephalisation in Felidae

Studied were the intraspecific and interspecific relationships between brain weight and body weight in Felidae. Inclination values of the allometric lines: intraspecific $\sim 0,25$, interspecific 0,566. Modern species of felids nearly have the same degree of cephalisation, deviations from the interspecific allometric line are only small. A comparison with brain sizes of fossil felids lead to the result: A threefold increase of brain size has taken place from Oligocene paleofelids to modern species.

Einleitung

Bestimmungen und Vergleiche der Hirngröße sind ein erster Schritt bei Studien zur vergleichenden Neuroanatomie und Hirnevolution. Voraussetzung für die Beurteilung der Hirngröße ist die Kenntnis der Beziehungen zwischen Hirn- und Körpergröße; sie können in den verschiedenen Größenreihen erfaßt werden mit der Allometrieformel: $HG = b \times KG^a$ (logarithmiert: $\log HG = \log b + a \times \log KG$)³. a kennzeichnet die von der Körpergröße abhängigen Hirngrößenunterschiede, b enthält die Faktoren, welche

¹ Herrn Prof. BERNHARD RENSCH als Dank für die vielen Anregungen zu Fragen der Allometrie und Hirnevolution zum 85. Geburtstag gewidmet. – ² Mit Unterstützung des Niedersächsischen Ministeriums für Wissenschaft und Kunst.

³ HG = Hirngewicht, KG = Körpergewicht.